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REPRODUCTIVE BIOLOGY OF GOODYERA
OBLONGIFOLIA (ORCHIDACEAE)

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Discovery of a large population of *Goodyera oblongifolia* Raf. prompted this investigation. Since some northern temperate orchids are known to have replaced or supplemented allogamy (cross-pollination) with autogamy (self-pollination) and asexual reproduction, the question arose as to what adaptations contributed to the success of the study population. Interrelations of vegetative propagation, self-compatibility, seed fertility, flower aggregation, nectar production, capsule development, pollination mechanisms, and pollinator distributions are considered.

Goodyera oblongifolia is distributed from Arizona to southeastern Alaska and east across Canada to the Great Lakes region. Disjunct populations occur in northeastern Mexico and in the vicinity of the St. Lawrence Seaway. Correll (1950) and Szczawinski (1969) reported *G. oblongifolia* abundant in certain localities and noted that the species spreads rapidly once established. In northern California, local populations of *G. oblongifolia*, growing in coniferous forests, consist of several to many colonies.

There are a few accounts of pollinators of the genus. Several authors observed *Bombus* pollinating *Goodyera repens* L. (Muller, 1873; Darwin, 1877; Hagerup, 1952) and Kipping (1971) observed *Bombus vosnesenskii* Rad. workers carrying pollinia and visiting *G. oblongifolia* in the Sierra Nevada. Kipping also captured *B. mixtus* Cresson visiting the orchid but it bore no pollinia.

Autogamy and agamospermy occur in several northern temperate orchids. Hagerup (1952) found bud autogamy in several orchids of Denmark, including *G. repens*. Agamospermy, the production of seeds without the fusion of gametes, occurs in at least five genera of the Spiranthinae (Hagerup, 1945 and 1947; Swamy, 1946 and 1948; Maheshwari and Narayanaswami, 1953). Neither agamospermy nor autogamy has been reported in *Goodyera oblongifolia* (also Spiranthinae).

MATERIALS AND METHODS

The study population consisted of several thousand plants located in a beach pine (*Pinus contorta* Doug. ex Loud.) climax forest community adjacent to coastal sand dunes, 3 km north of Manila, Humboldt County (T6N R1W Sec. 23 and 26), California. Ten 1 m² plots were staked for studies to determine percent capsule set and capsule maturation time, to record phenology of the population, and to evaluate floral density. Once or twice a week the number of buds, flowers, and capsules in each plot were recorded. Vouchers were deposited in HSC.

From outside the plots, two hundred plants, half flowering and half not flowering, were examined for number of new growths. In assessing vegetative propagation, only plants with a single, well developed basal rosette were used.

Self-compatibility and insect-exclusion experiments were designed. Five potted plants from the study population were placed in a screened room and tested for self-compatibility. Flowers were hand-pollinated by placing a pollinarium on the stigmatic surface. To determine if the species self-pollinated, I placed 12 potted plants in a cage that excluded all insects. Plants in this experiment were initially sprayed with a garden sulfur solution to rid them of insects.

Seed fertility was estimated for all capsules developed in the insect-exclusion and self-compatibility experiments, as well as for the capsules of ten naturally pollinated flowers collected from the study population. The technique used was much the same as that employed by Stort

(1973) and L. Thien (pers. comm., 1973). For each capsule, five slides were made and nine fields from each slide were viewed, $40\times$. A seed was considered fertile if it contained a developed embryo.

Pollinator effectiveness and pollination mechanics were assessed by observing pollinator behavior and by dissecting 341 variously aged fresh flowers and 128 withered flowers, all selected from the study population. Position of the column in relation to the lip (labellum), stickiness of the stigma and the viscidium, absence of pollinia, and presence of pollen on the stigma were noted for each fresh flower examined. Presence or absence of pollinia was also recorded for each withered flower.

Robbin Thorp (University of California, Davis) identified pollinators and deposited them in the UC Davis insect collection.

RESULTS

The ten-week flowering period of the study population began 8 August and ended 18 October 1973. Each flower lasted approximately two weeks. Capsules matured in six to eight weeks, measured from the time the perianth withered to capsule dehiscence. Table 1 contains data from the ten plots.

Plants that were flowering usually produced more new rhizomatous growths than plants that were not flowering. Of plants in flower, 13 had no new growths, most had either one or two, and four plants had three. Of plants not in flower, 77 had no new growths, 22 had one, and one plant had two. The mean number of new growths was 1.74 for flowering plants and 0.46 for those not flowering.

The insect-exclusion experiment tested 111 flowers and 9.0 percent formed capsules; however, all fruits were parthenocarpic and from the same inflorescence. All hand-pollinated flowers in the self-compatibility

TABLE 1. FLOWER DENSITY AND PERCENT CAPSULE SET FROM A POPULATION OF *GOODYERA OBLONGIFOLIA*. Data are from 1 m² plots. See text for study population locality.

Plot	Plants flowering	Flowers	Flowers per inflorescence		Capsule set (%)
				Capsules	
1	8	133	16.6	70	52.6
2	11	104	9.4	70	67.3
3	7	75	10.7	28	37.3
4	15	207	13.8	105	50.7
5	18	202	11.2	27	13.3
6	17	197	11.6	104	52.7
7	15	208	13.8	120	57.6
8	9	98	10.9	22	22.7
9	18	218	12.1	124	56.8
10	9	118	13.1	52	44.0
Totals	127	1560	ave. = 12.3	722	ave. = 46.2

experiment developed fruit. Mean seed fertility was 52.7 percent (6,132 seeds from 14 capsules). Seed fertility of individual capsules varied from 2.1 to 98.8 percent. Examination of 4,874 seeds from ten fruits of naturally pollinated flowers showed 83.8 percent average seed fertility. Percent seed fertility for these capsules ranged from 62.7 to 96.6.

A few polyembryonic seeds were observed in capsules of high seed fertility. Polyembryony, not a rare phenomenon in orchids, is also known to occur in *G. tessellata* Lodd. and *G. pubescens* (Willd.) R. Br. (Leavitt, 1901). As defined by Wirth and Withner (1959), seeds with multiple embryos all derived from the same egg cell are polyembryonic. Although not proven by embryological studies, those few seeds were considered polyembryonic because the two embryos, and never more than two, were always partially fused. The low frequency of these seeds makes them insignificant to the reproductive biology of *G. oblongifolia*.

Queens of *Bombus occidentalis* Greene, laden with pollinia, were observed and captured while pollinating the orchid. Few bumblebees were seen visiting the population and were rarely observed on overcast days. Bees briefly visit several flowers per inflorescence, often working the lower flower first.

Goodyera oblongifolia is protandrous; pollen deposition is temporarily prevented by the close proximity of the column to the lip. When the flower opens, the column is horizontal relative to the labellum (fig. 1). In this position, the median groove of the lip forms a narrow tube with the elongate rostellum and viscidium. When a bee lands on the flower and probes for nectar, its galea contacts the sticky viscidium, which adheres to the bee's mouth parts so that the bee will leave the flower carrying pollinia. The narrow tube is large enough for the bee's probing proboscis but too small if the proboscis bears pollinia. A bee carrying pollinia is prevented from pollinating a young flower because the position of the column blocks access to the stigma. As the flower ages, the column becomes vertical and the viscidium, if still present, dries (fig. 1). If bees carrying pollinia visit such flowers, pollinia come in contact with the stigma and small chunks of pollen from the sectile pollinia are left on the stigma.

In 128 withered flowers, pollinia were missing in 44.5 percent. Pollen was found on 58.6 percent of stigmas in 181 wild fresh flowers with vertical columns. Capsules matured in 46.2 percent of the flowers from the ten plots studied (Table 1), notably less than the percentage of flowers pollinated. It is unlikely that the pollen found on the stigmas was foreign. In the vicinity of the *Goodyera* population, only two other orchids were flowering concurrently: *Piperia elegans* (Lindl.) Rydb. and *P. maritima* (Greene) Rydb. These two closely related piperias are probably adapted for moth pollination; pollinia are not likely to be transferred from them to *G. oblongifolia*.

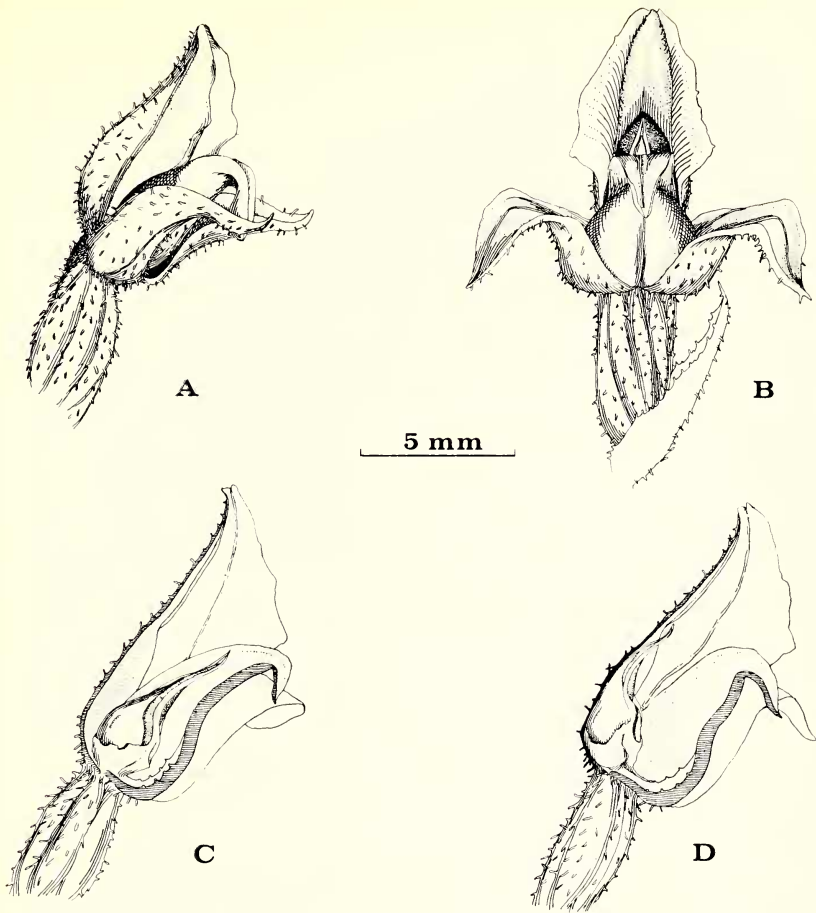


FIG. 1. Flowers of *Goodyera oblongifolia* Raf. A, side view; B, front view; C and D, perianth sectioned showing horizontal and vertical column positions.

DISCUSSION

Although parthenogenesis has been reported in related genera, I found no evidence for it in *G. oblongifolia*. Asexual reproduction, excluding vegetative propagation, probably does not occur in this species.

The capsule maturation period was short; the time interval between pollination and fertilization, although not determined, was correspondingly brief. Swamy (1949) suggested that a short time lapse between pollination and fertilization represents a primitive condition in the family. This may not necessarily be primitive but may have evolved secondarily in response to environmental conditions. The number of *G. oblongifolia* capsules that matured and dehisced was fewer than the

number of flowers pollinated. Whatever the mortality rate, it would be higher if the capsules had to weather the winter.

Rhizomes of *Goodyera* produce leaves until terminated by an inflorescence (Stoutamire, 1974; Luer, 1975). For *G. oblongifolia*, a plant that flowers usually dies before the next flowering season. Loss of that member from the population is compensated since both flowering and non-flowering individuals reproduce vegetatively and a plant in flower usually develops more new growths than one not flowering. New growths become independent prior to senescence of the parent plant. This allows development of colonies exclusively by vegetative reproduction, which may be particularly important to very small populations where chances of pollination are diminished.

For potentially greater seed production, self-compatibility is advantageous for prolific clonal species (Estes and Brown, 1973; Estes and Thorp, 1974). Kipping (pers. comm., 1973) and I found *G. oblongifolia* to be self-compatible, although in my experiment, seed fertility (not determined by Kipping) dropped radically for some capsules. Nevertheless, mean fertility is high, indicative of self-compatibility. Chances of successful sexual reproduction in this species are not hindered by the combination of self-incompatibility and clonal populations.

Vegetative reproduction and self-compatibility are adaptive in *G. oblongifolia*, but they are also factors that can be detrimental to the genetic balance and plasticity of the species. Darwin (1877) and Gray (1862) suggested that inflorescences of *G. repens* are protandrous as a whole. Pollinia-carrying bees visit lower flowers first, pollinating them as they work up the inflorescence. Before leaving, the insect removes pollinia from the protandrous upper flowers; it then carries its new load to the next inflorescence. This was often the observed behavior of bees pollinating *G. oblongifolia*. The weakly protandrous inflorescence does not guarantee outcrosses nor do protandrous flowers because of the clonal population structure. The genetic effect of many pollinations is similar to autogamy; therefore much inbreeding occurs despite protandry. Nevertheless, outcrosses likely happen occasionally, thereby sporadically regenerating genetic variability in colonies of *G. oblongifolia*.

Results of the insect-exclusion experiment are negative: autogamy presumably does not occur.

The pollination mechanism described for *G. oblongifolia* is essentially the same as that discussed by Kipping (1971). Luer (1975) attributes this mechanism to North American representatives of *Spiranthes* and *Goodyera*. Contrary to my observations, Luer suggests that the mechanism of protandry involves a movement of the lip instead of the column.

Pollinators are likely to make repeated visits to flowers offering a food source. For example, a low percent capsule set was reported for orchids employing deception to lure pollinators (Mosquin, 1970; Thien and Marcks, 1972). In contrast, *G. oblongifolia* has a relatively high capsule set (Table 1). Nectar offered at the base of the saccate lip probably

encourages repeated pollinator visits.

As many as 30 flowers are aggregated on a raceme but racemes with 10–15 flowers are more common (Table 1). The clonal population structure clusters inflorescences so that the nectar producing flowers are grouped. The adaptive effects of flower aggregation, although relatively weak in *G. oblongifolia*, may be an increase in odor strength and visual stimulus and a localization of a food source.

Ranges of the three known pollinators, *Bombus mixtus*, *B. vosnesenskii*, and *B. occidentalis*, are sympatric with the western region of the orchid's distribution (Muesebeck et al., 1951). It is probable that several other species of *Bombus*, and maybe species of related genera, pollinate *G. oblongifolia* in western North America. Because this orchid is adapted to a group of commonly occurring pollinators and because orchid seeds are wind dispersed, the potential for range extension is great. Isolated populations in northeastern United States and adjacent Canada and in Nuevo Leon, Mexico, are possible realizations of that potential. However, Case (1964) believes disjunct populations in the Great Lakes Region are remnants of a once widespread distribution broken by glaciation. This reasonable suggestion does not refute the potentialities of successful long distance dispersal.

The short capsule maturation time minimizes capsule mortality during development. Self-compatibility, flower aggregation, nectar production, and adaptation to commonly occurring pollinators contribute to a greater number of pollinations. Protandry encourages outcrossing and so contributes to the maintenance of genetic variability. Adaptation to a widespread pollinator group and capabilities for vegetative propagation improve chances of successful establishment of new populations. These interactions are partially responsible for the success of the species.

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TAXONOMIC AND MORPHOLOGICAL OBSERVATIONS ON *BOTRYCHIUM MULTIFIDUM* (OPHIOGLOSSACEAE)

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Once upon a time, Clausen (1938) recognized five subspecies of *Botrychium multifidum* (Gmel.) Rupr. although he acknowledged that they grade insensibly into one another especially where their ranges are confluent. For example, the North American range of ssp. *silatifolium* (Presl) Clausen is from the Sierra Nevada to the Pacific Northwest and across